

Species of *Pleurosigma* (Pleurosigmataceae) with lanceolate or slightly sigmoid valve outlines: analysis of type material

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The type material of seven taxa of *Pleurosigma* W. Smith were studied, including *P. atlanticum* Heiden & Kolbe, *P. chilense* Hustedt & Krasske, *P. chilensis* var. *patagonica* Ferrario & Sar, *P. indicum* Simonsen, *P. intermedium* W. Smith, *P. nubecula* W. Smith and *P. simonsenii* Hasle. All these taxa are mainly characterized by a straight or almost straight valve outline. The fine morphology of the type specimens is studied and compared with similar taxa, and appropriate taxonomic changes are proposed. The material examined included the lectotypes of *P. chilense* and *P. atlanticum*, the holotypes of *P. indicum* and *P. simonsenii* from the Friedrich Hustedt Center for Diatom Research (BRM, Germany), the isoelectotypes of *P. intermedium* and *P. nubecula* from the Van Heurck Collection (BR, Belgium), and the holotype of *P. chilensis* var. *patagonica* and material of *P. simonsenii* collected in Argentinian coastal waters from the Herbarium of the División Ficología (LPC, Argentina). Based on light and scanning electron microscope analyses, it was concluded that *P. atlanticum*, *P. chilense*, *P. indicum*, *P. intermedium* and *P. simonsenii* are valid species, *P. nubecula* is a heterotypic synonym of *P. intermedium* and *P. chilensis* var. *patagonica* must be raised to specific rank under the name *P. patagonicum* (Ferrario & Sar) Sterrenburg & Sar stat. nov. as it differs from *P. chilense* in the fine morphology of the external central raphe fissures, the valve apex and the areolae near the centre.

Keywords: morphology, *Pleurosigma* species, taxonomy, type material

Introduction

The genus *Pleurosigma* was first described by Smith (1852) and characterized by having valves convex, sigmoid and striated, with striae visible as dots. Smith (1852) established two sections in the genus, one characterized by transverse and oblique striae and the other with transverse and longitudinal striae. According to Smith (1856) the name *Pleurosigma* was given despite the fact that the genus *Gyrosigma* Hassall had been previously described ‘for the designation of this division of the Naviculaceae’ because he considered it an inappropriate name as it was difficult to pronounce (sic!). Although *Gyrosigma* is the earliest legitimate name with the same rank, most classical authors such as Ralfs in Pritchard (1861), Grunow in Cleve & Grunow (1880), Van Heurck (1880–1885), Peragallo (1891) and Peragallo & Peragallo (1897–1908), adopted the name *Pleurosigma sensu lato*. Cleve (1894) formally split the genus *Pleurosigma sensu lato* into *Pleurosigma sensu stricto* for those taxa with transapical and oblique striae, and *Gyrosigma sensu stricto* for those with transapical and longitudinal striae.

The genus *Pleurosigma* W. Smith is a conserved name against *Scalprum* Corda, *Gyrosigma* and *Endosigma*

Brébisson, which were designated as taxonomic synonyms and rejected (Lanjouw et al. 1956). Additionally, *Gyrosigma* Hassall is conserved against *Scalprum*, which is a taxonomic synonym and rejected name, when it is not considered a synonym of *Pleurosigma*. Therefore, the name *Gyrosigma* was restored because it is the name of a taxon at the same rank, distinct from that of the *nomen conservandum*, in this case *Pleurosigma sensu stricto*.

Since Smith (1852) did not designate the type species for the genus *Pleurosigma*, Boyer (1927) lectotypified it with *P. angulatum* (Quekett) W. Smith and *Navicula angulata* Quekett as the basionym. Nevertheless, as no specimen was found in Quekett’s original material and the illustration in the protologue differs from the currently understood concept of *P. angulatum*, Ross & Sterrenburg (1996) proposed the designation of a conserved type for *N. angulata* from the W. Smith Collection (slide BM 23671, *typus conservandus*: Northern Ireland, Belfast, August 1849) allowing the continued current usage of the name *P. angulatum* (Compère 1999, Greuter et al. 2000).

According to VanLandingham (1978), *Pleurosigma sensu stricto* contains 90 validly published taxa. Subsequently, Round et al. (1990) and Sterrenburg (1991a)

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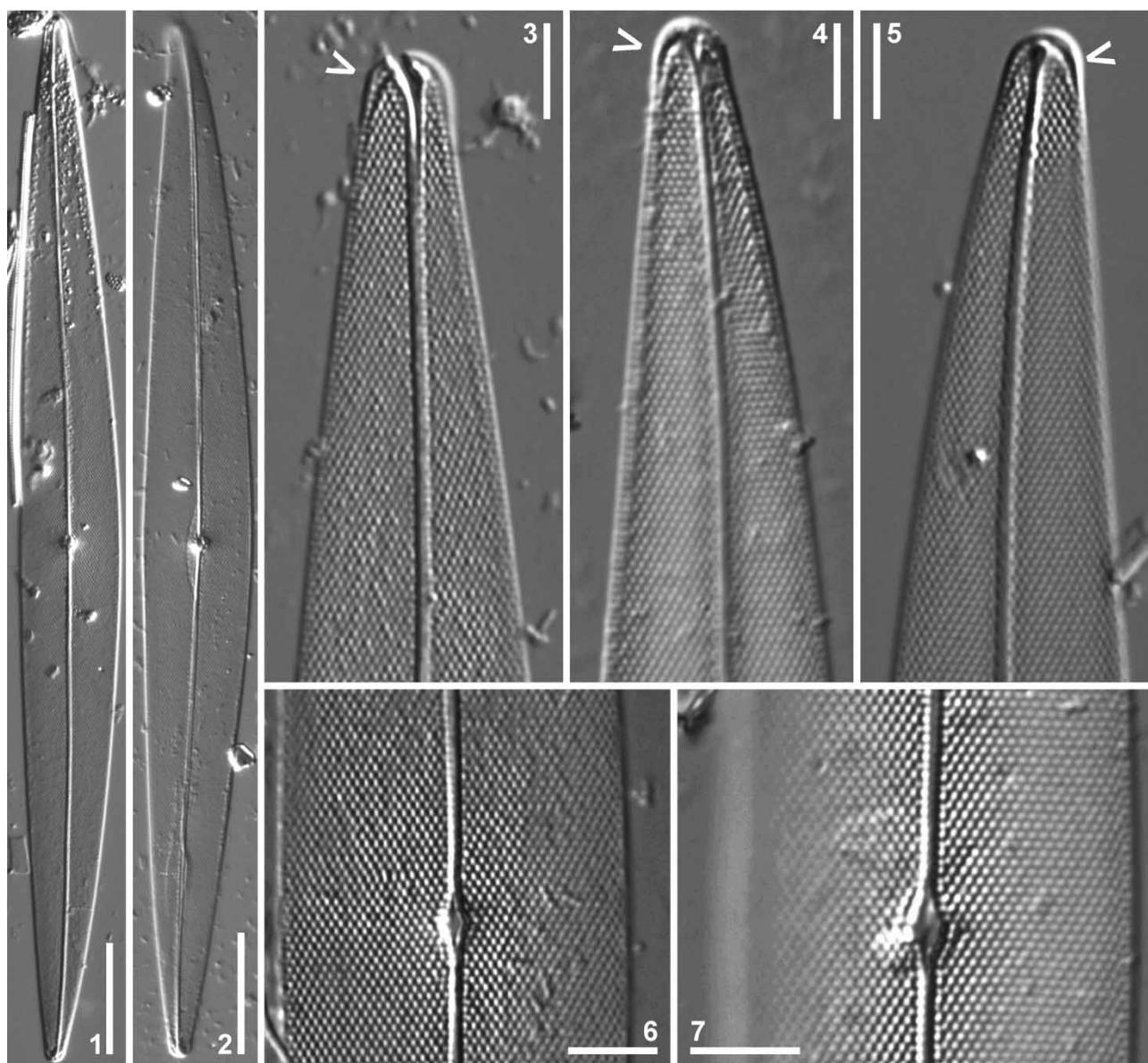
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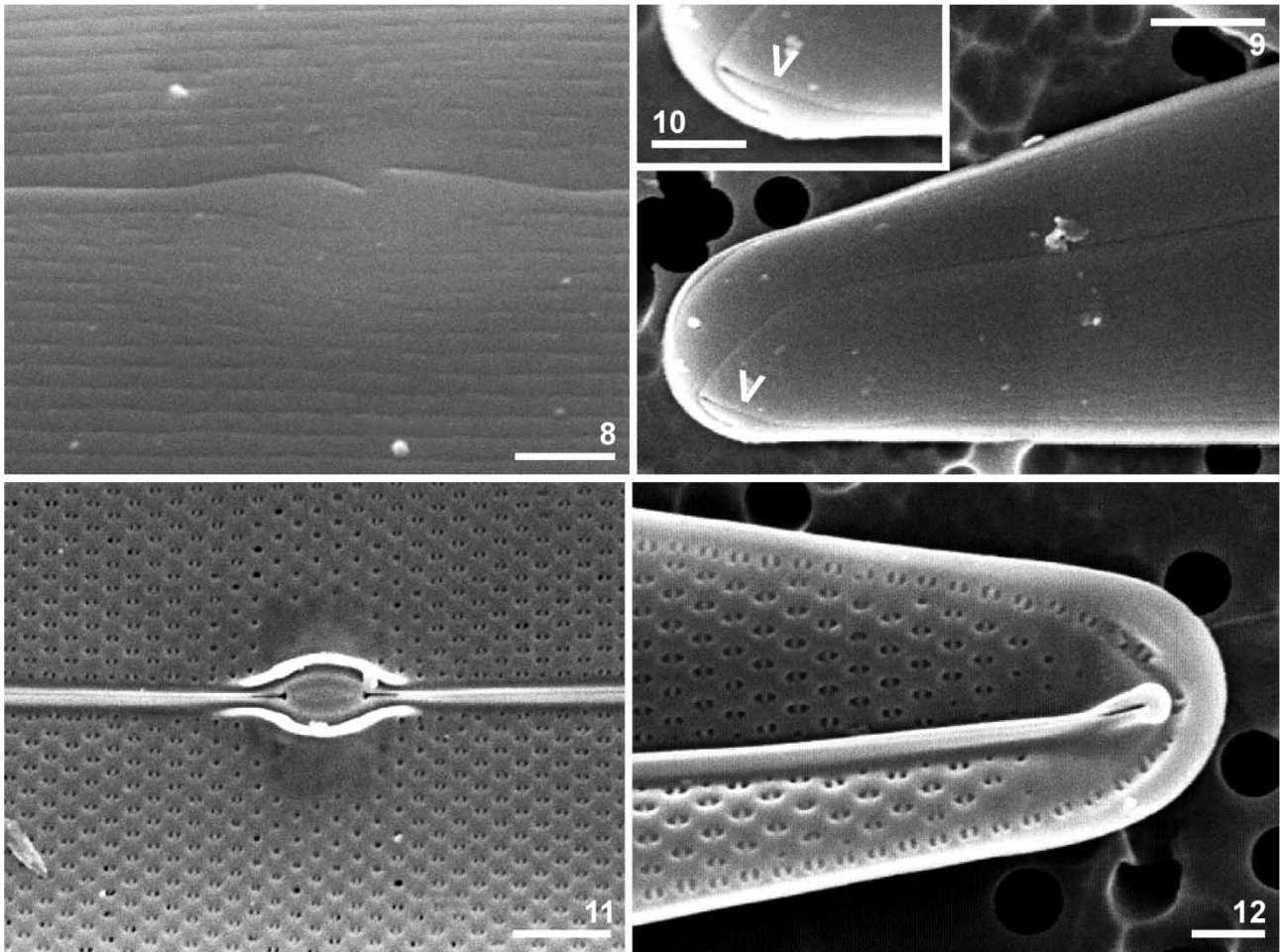
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pointed out that the genus urgently needed revision. Diagnostic features for separating species of *Pleurosigma* with light microscopy (LM) were summarized and discussed by Sterrenburg (1991a) and additionally new criteria for species characterization with scanning electron microscopy (SEM) were proposed by Cardinal *et al.* (1989) and Sterrenburg (1991b). Critical investigations of original material (e.g., Sterrenburg 1991b, 2001, Reid 2001, Stidolph 2002, Sterrenburg *et al.* 2003) help to clarify some taxonomical problems and several new species were described (e.g., Ferrario & Sar 1990, Sterrenburg 1991a, b, 2001, Sterrenburg *et al.* 2000, 2003, von Quillfeldt 2000, Reid 2001, 2002) based on ultrastructural features.

Although *Pleurosigma* is usually described as having a sigmoid valve outline and raphe, it contains a group of 20 taxa which are narrowly or rhombic lanceolate, or only very slightly sigmoid towards the poles, with more or less acute apices and a straight or only very slightly eccentric (towards the apices) raphe–sternum, such as: *P. acus* Mann, *P. angusticonvexum* Hagelstein, *P. antarcticum* Grunow, *P. atlanticum* Heiden & Kolbe, *P. chilense* Hustedt & Krasske, *P. chilensis* var. *patagonica* Ferrario & Sar, *P. directum* Grunow, *P. dolosum* Mann, *P. eudon* Pantocsek, *P. glacialium* Simonsen, *P. observatoriensis* Simonsen, *P. indicum* Simonsen, *P. intermedium* W. Smith, *P. nico-baricum* Grunow, *P. nubecula* W. Smith, *P. observatoriensis*



Figs 1–7. *Pleurosigma intermedium*, isolectotype material, LM. **Figs 1–2.** General view of two valves. **Figs 3–5.** Apices of three valves showing calcars (arrowheads). **Figs 6–7.** Detail of the valve at centre showing the external raphe fissures in Fig. 7. Scale bars = 20 µm (Figs 1–2); 5 µm (Figs 3–7).



Figs 8–12. *Pleurosigma intermedium*, isolectotype material, SEM external (Figs 8–10) and internal views (Figs 11–12). **Fig. 8.** Central part of the valve showing raphe fissures. **Fig. 9.** Valve apex showing a terminal raphe fissure and calcar (arrowhead). **Fig. 10.** Detail of apex with a calcar (arrowhead). **Fig. 11.** Valve centre showing proximal raphe ends and nodule bordered by two thin bars. **Fig. 12.** Valve apex showing recessed area with apical slits. Scale bars = 2 μm (Figs 9, 11); 1 μm (Figs 8, 10, 12).

Simonsen, *P. peragalli* Brun, *P. sagitta* Tempère & Brun, *P. simonsenii* Hasle, *P. simplex* Ricard and *P. subrectum* Cleve.

The present study focuses on the morphology and taxonomy of *P. atlanticum*, *P. chilense*, *P. chilensis* var. *patagonica*, *P. indicum*, *P. intermedium*, *P. nubecula* and *P. simonsenii*. The main objective of this study is to document the morphological features of the taxa based on the examination of type material, compare with similar taxa and propose any necessary taxonomic changes.

Materials and methods

The slides and samples used for this study are listed below.

Pleurosigma chilense. Lectotype and isolectotype, sample AM461, slides 297/56 and 297/57, respectively, from Calbuco, Chile, collected by G.H. Schwabe, 27 November 1937 (Krasske No. 4310) in the Hustedt Collection (BRM). Type material from sample AM461 was used for SEM analysis.

Pleurosigma indicum. Holotype, sample SM338, slide SIM64/45, from station 103 (170 m deep, 11°27.5'N by 53°04.5'E) in the Arabian Sea, collected by R. Simonsen, 20 December 1964, in the Simonsen Collection (BRM). Type material from sample SM338 was used for SEM analysis.

Pleurosigma simonsenii. Holotype, sample SM338, slide SIM64/45, from station 103 (170 m deep, 11°27.5'N by 53°04.5'E) in the Arabian Sea, collected by R. Simonsen, 20 December 1964. Additional material quoted by Simonsen (1974) in the protologue: sample SM603, from station 217 (120 m deep, 18°45.3'N by 70°18'E), collected by him, 1 March 1965, in the Simonsen Collection (BRM), was prepared for SEM analysis.

Pleurosigma atlanticum. Lectotype, slide 284/50, Gauss-Expedition, Atlantic Ocean, 19 August 1903, 400 m, 27°18'S by 02°51'E and additional material, slide 284/48, Gauss-Expedition, Atlantic Ocean, 18 August 1903, 200 m Nansen net, 28°22'S by 04°09'E, deposited at BRM.

Table 1. Comparison of the biometric data and some morphological features in the studied species of *Pleurosigma* from literature and type material examination.

Taxon	Reference	Length (μm)	Width (μm)	Transapical striae in 10 μm	Oblique striae in 10 μm		Stria angle		Raphe–sternum	Apices	Valve outline
					Centre	Poles	Centre	Poles			
<i>P. atlanticum</i>	Heiden & Kolbe (1928)	69–76	13.0–16.5	20		20		60°	Slightly deflected at poles; raphe angle +1.2°	Blunt rounded obtuse	Lanceolate
	This study	72–87	15.4–16.3	20–22		19–20		45–47°	Very slightly deflected; raphe angle +1.2°	Rounded obtuse	Lanceolate
<i>P. chilense</i>	Krasske (1941)	110–140	15–19	28		28		n.d.	Straight, slightly eccentric at poles	Acute	Narrowly lanceolate, straight barely sigmoid at the apices
	Simonsen (1987)	145–146	20	n.d.		n.d.	n.d. 54–59°*	n.d. 57–59°*	Straight, deflected at poles	Very acute	Narrowly lanceolate, almost straight
	Lange-Bertalot et al. (1996)	141*	16*	29*	27*	n.d.	60°*	n.d.	Straight, deflected at poles	Very acute	Narrowly lanceolate, almost straight
	This study	103–133	14–17	29–33	27–32	27–33	54–59°	51–56°	Straight, slightly eccentric at poles; raphe angle 0°	Very acute	Lanceolate, slightly sigmoid near the end
<i>P. chilensis</i> var. <i>patagonica</i>	Ferrario & Sar (1991)	146–225	17–23	24–28		24–28	57°*	64°*	Straight, slightly eccentric at poles	Acute	Narrowly lanceolate, straight
	This study	189–229	17.0–20.6	26–30	23–26	23–29	57–66°	56–62°	Straight, not eccentric towards the ends; raphe angle 0°	Acute	Narrowly lanceolate to sub-rhomboidal, straight
<i>P. indicum</i>	Simonsen (1974)	70–90	8–11	26–28		24		45°	Central in the middle, somewhat eccentric before the ends	Sub-acute	Lanceolate, slightly sigmoid
	This study	79.0–81.5	10–11	23–24		20–24		44–48°	Almost straight for most part of its length, becoming eccentric towards the ends; raphe angle +2.5–2.6°	Sub-acute	Lanceolate, slightly sigmoid near the apices
<i>P. intermedium</i>	Smith (1853)	167–223	20*	n.d.		21		n.d.	Very slight deflected	Acute	Lanceolate
	Hendey (1964)	168–194	17–18	n.d.		n.d.		n.d.	n.d.	n.d.	n.d.
	This study	172–190	18	21–22	20–22	20–23	60–63°		Very slightly deflected; raphe angle +1.2–1.8°	Acute	Narrowly lanceolate

<i>P. nubecula</i>	Smith (1853)	139–167	19*	n.d.	n.d.	Flexure hardly perceptible	Obtuse	Linear-lanceolate
	Hendey (1964)	126–146	17–18	n.d.	n.d.	n.d.	n.d.	n.d.
	This study	82–85	16	25–26	60–61°	Very slightly deflected; raphe angle +1.2–1.9°	Sub-acute	Narrowly lanceolate
<i>P. simonsenii</i>	Simonsen (1974)	300–600	40–75	28–30	60°	Sigmoid before the ends	Very acute	Lanceolate, slightly sigmoid near the ends
	Boalch & Harbour (1979)	400	45	n.d.	58°*	Straight, flexure near the apices	Very acute	Lanceolate, slightly sigmoid near the ends
	This study	250–598	30–73	30–32	56–60°	Straight, deflected near the apices; raphe angle +1.6–2.7°	Very acute	Lanceolate, slightly sigmoid near the end
	Material from Argentina	398–596	48–62	29–31	57–59°	Straight, deflected near the apices; raphe angle +1.9–3.1°	Very acute	Lanceolate, slightly sigmoid near the end

Note: n.d., no data; *, measured from micrographs.

Pleurosigma intermedium. Slide BR-4248, from Newhaven, Sussex, UK, deposited in the Van Heurck Collection (BR). The sample used for the slide was also prepared for SEM analysis.

Pleurosigma nubecula. Slide BR-4249, from Seaford, Sussex, UK, deposited in BR. The sample used for the slide was also prepared for SEM analysis.

Additionally, a slide prepared from the same locality and labelled as BR-4249 (Sterrenburg private collection) was used for LM study.

Pleurosigma chilensis var. *patagonica*. Holotype, slide 3613, from the Caleta Valdés, Chubut, Argentina, unknown collector, 25 August 1981, deposited in LPC. Type and additional material mentioned in the protologue, sample 3624, from the Caleta Valdés, Chubut, Argentina, unknown collector, 20 October 1981, deposited in LPC, were prepared for SEM analysis.

In addition to the above type material, more recent samples from Argentinian coastal waters collected from several localities in the Province of Buenos Aires were analysed. Surface water (0–5 m) samples were collected with a 30 µm mesh-size plankton net and fixed with 4% formalin. The preserved samples were rinsed with distilled water to remove salt and formalin, and the organic matter was then oxidized according to Prygiel & Coste (2000). The cleaned material was mounted for LM and SEM according to Ferrario et al. (1995). Permanent mounts were made with Hyrax or Naphrax and slides were deposited in the Herbarium at the Universidad Nacional de La Plata (LPC): LPC 11098, Pinamar, LPC 11099, Villa Gesell and LPC 11100, Mar Azul.

Microscopic investigation of all slides was carried out under phase and differential interference contrast optics using a Nikon Microphot-FX, Leica DM 2500 and Axioplan D 7082 LM with camera SIS color view III. Scanning electron microscopy was performed with Jeol JSM 6360 LV, ISI-DS 130 SEM and Fei Quanta FEG 200 microscopes.

Terminology follows that recommended by Ross et al. (1979), Round et al. (1990) and Sterrenburg (1991a, b). The term calcar was introduced by Sterrenburg in Stidolph (1992) and further discussed by Sterrenburg et al. (2003).

Results

Pleurosigma intermedium W. Smith (Figs 1–12, Table 1)

Protologue. Smith 1853, p. 64, pl. 21, fig. 200.

Description. Valves delicate, lanceolate, barely sigmoid near the apices, gradually tapering towards the ends, only slightly vaulted, with acute ends (Figs 1–2), 172–190 µm long, 18 µm wide (three valves observed). Raphe–sternum almost straight for most of its length, becoming somewhat eccentric with minimal curvature near the apices (Figs 1–2). Terminal areas very small, unilaterally dilated,

funnel-shaped, in apical position (Figs 3–5). One calcar visible in LM as a spur-like shadow at the apex (Figs 3–5, arrowheads). Raphe angle $+1.2$ – 1.8° . Central area very small, oval, symmetrical (Figs 6–7). Central and terminal raphe fissures not reliably visible in LM. Transapical striae parallel 21–22 in $10\ \mu\text{m}$, oblique equally fine 20–23 in $10\ \mu\text{m}$. Oblique striae intersecting at a 60 – 63° angle.

External and internal details of the raphe clearly visible in SEM (two valves observed) (Figs 8–12). External central raphe fissures very approximate, one longer and more markedly curved than the other (Fig. 8) and terminal raphe fissures hook-shaped (Figs 9–10), oppositely bent (Figs 1–2). Sternum slightly thickened internally, central nodule with two bars, one slightly longer than the other, internal central raphe endings dilated as a small triangle, coaxial (Fig. 11). Helictoglossae surrounded by a recessed area with apical slits (Fig. 12). Calcar externally visible

as a long accessory fissure ending near the hooked part of the raphe fissure (Figs 9–10). Internally areolae elliptical, bisected by a narrow silica bar over most of the valve (Figs 11–12), roundish without bars in a small area around the central nodule (Fig. 11). Areola opening externally as apically oriented slit-like foramina (Fig. 8). A continuous series of elliptical bisected areolae is present at the valve margin (Fig. 12).

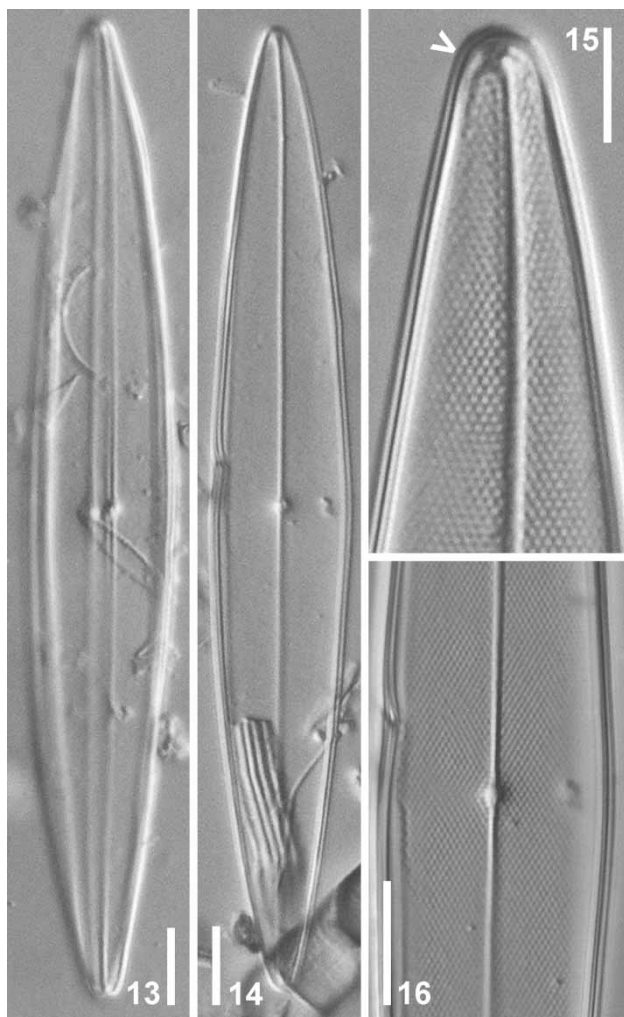
Remarks. This was the first straight *Pleurosigma* species described (Smith 1853). Material from Baie des Chaleurs, Canada illustrated by Cardinal *et al.* (1986: 184, figs 58–60) matched the type material in morphometric data and internal ultrastructural details. Additional specimens from Spain (Sterrenburg Collection No. 569, Ria de Arosa, Spain) and The Netherlands (Sterrenburg Collection No. 149, Grevelingen, Zeland) contained specimens matching the description above, with valve length ranging from 100 to $160\ \mu\text{m}$ (data not shown).

Pleurosigma nubecula W. Smith (Figs 13–20, Table 1)

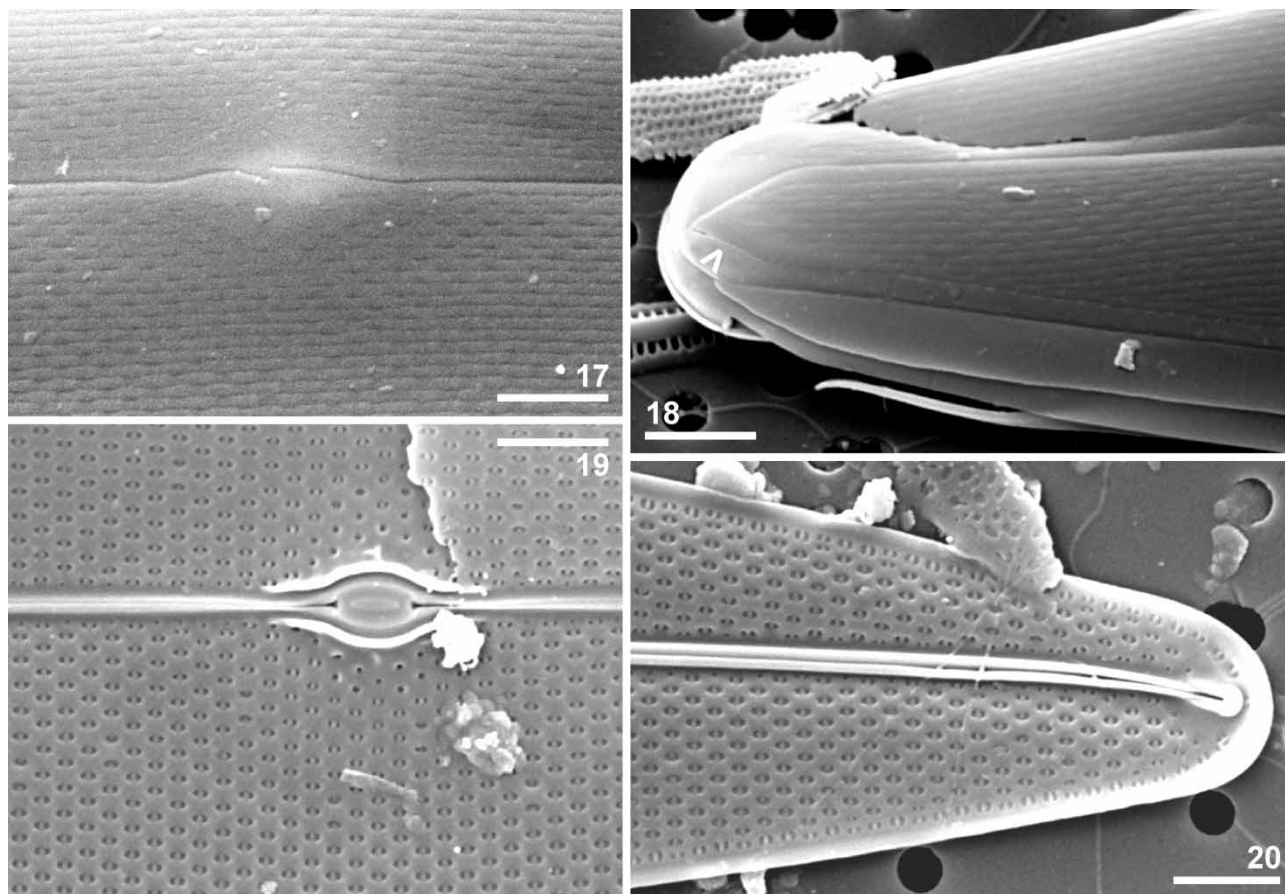
Protologue. Smith 1853, p. 64, pl. 21, fig. 201.

Description. Valves delicate, lanceolate, barely sigmoid, tapering gradually towards the ends, only slightly vaulted, with gently rounded ends (Figs 13–14), 82 – $85\ \mu\text{m}$ long, $16\ \mu\text{m}$ wide (one frustule and one valve observed). Raphe–sternum straight except for a minimal single curvature near the apices, where it becomes slightly eccentric (Figs 13–15). Terminal areas very small, unilaterally dilated, funnel-shaped, in apical position (Fig. 15). One calcar visible in LM as a spur-like shadow at the apex (Fig. 15, arrowhead). Raphe angle $+1.2$ – 1.9° . Central area small, oval, symmetric (Figs 13–14, 16). Central and terminal raphe fissures not reliably visible in LM. Transapical striae parallel 25 – 26 in $10\ \mu\text{m}$, oblique striae, 23 – 25 in $10\ \mu\text{m}$, intersecting at a 60 – 61° angle.

External and internal details of the raphe clearly visible in SEM (two valves observed) (Figs 17–20). External central raphe fissures very approximate, one longer and more markedly curved than the other (Fig. 17). External terminal raphe fissures hook-shaped (Fig. 18), oppositely bent (Figs 13–14). Sternum slightly thickened internally, central nodule with two bars, one slightly longer than the other, internal central raphe endings dilated as a small triangle, coaxial (Fig. 19). Helictoglossae surrounded by a recessed area with apical slits (Fig. 20). Calcar externally visible as a long accessory fissure ending near the hooked part of the raphe fissure (Fig. 18, arrowhead). Internally areolae elliptical, bisected by a narrow silica bar over most of the valve (Figs 19–20), and roundish without bars in a small area around the central nodule (Fig. 19). Areola opening externally as apical slit-like foramina (Fig. 17). A continuous series of elliptical bisected areolae is present at the valve margin (Fig. 20).



Figs 13–16. *Pleurosigma nubecula*, isolectotype material, LM. **Fig. 13.** Valve view of a frustule. **Fig. 14.** Whole valve. **Fig. 15.** Apex of a valve showing calcar (arrowhead). **Fig. 16.** Central region of a valve showing a small, oval, central area. Scale bars = $10\ \mu\text{m}$ (Figs 13–14, 16); $5\ \mu\text{m}$ (Fig. 15).



Figs 17–20. *Pleurosigma nubecula*, isolectotype material, SEM external (Figs 17–18) and internal views (Figs 19–20). **Fig. 17.** Central part of the valve showing raphe fissures. **Fig. 18.** Valve apex showing a terminal raphe fissure and calcar (arrowhead). **Fig. 19.** Valve centre showing proximal raphe ends and nodule bordered by two thin bars. **Fig. 20.** Valve apex showing helictoglossa surrounded by recessed area with apical slits. Scale bars = 2 μm .

Remarks. Smith (1853) described this taxon immediately after *P. intermedium* and gave a continuous size range and the same stria density for both species. Hendeby (1964) analysed the type material of *P. intermedium* and *P. nubecula* in LM and noted that specimens of the former were consistently longer than those of the latter. The three type specimens of *P. intermedium* that we found do not attain the maximum size given in the protologue. Clearly, Smith (1853) observed a larger number of specimens than Hendeby (1964) and we found.

Pleurosigma atlanticum Heiden & Kolbe (Figs 21–23, Table 1)

Protologue. Heiden & Kolbe 1928, p. 647, pl. 4, fig. 93 nec Frenguelli 1928, p. 507, pl. 1. fig. 5.

Description. Valves lanceolate, gradually tapering towards the obtuse rounded ends (Figs 21–22), 72–87 μm long, 15.4–16.3 μm wide. Raphe–sternum straight, slightly curved at the ends in opposite direction (three valves observed) (Figs 21–22). Terminal area funnel-shaped in apical position (Fig. 23). Raphe angle $+1.2^\circ$. Central area

very small, inconspicuous. Central and terminal raphe fissures not visible in LM. Transapical striae parallel 20–22 in 10 μm , oblique striae, 19–20 in 10 μm , intersecting at a $45\text{--}47^\circ$ angle.

Remarks. As pointed out by Sar et al. (2009), two different taxa were described under the same name *P. atlanticum* by Heiden & Kolbe (1928) and Frenguelli (1928). As far as we can determine, neither taxon has been reported since. Simonsen (1992) selected Heiden & Kolbe slide 284/50 from the Gauss-Expedition conducted in the Atlantic Ocean, as the lectotype and pointed out that the unprocessed material deposited at the Botanical Museum in Berlin was destroyed during World War II, thus, no type material is available for SEM.

Pleurosigma chilense Hustedt & Krasske (Figs 24–36, Table 1)

Protologue. Krasske 1941, p. 274, pl. 5, fig. 7a–b, as *P. chilensis*. Name corrected by Simonsen 1987, p. 265.

Description. Valves delicate, lanceolate, tapering gradually towards the ends, rather flat although slightly vaulting near the acute apices, 103–133 μm long, 14–17 μm wide (10

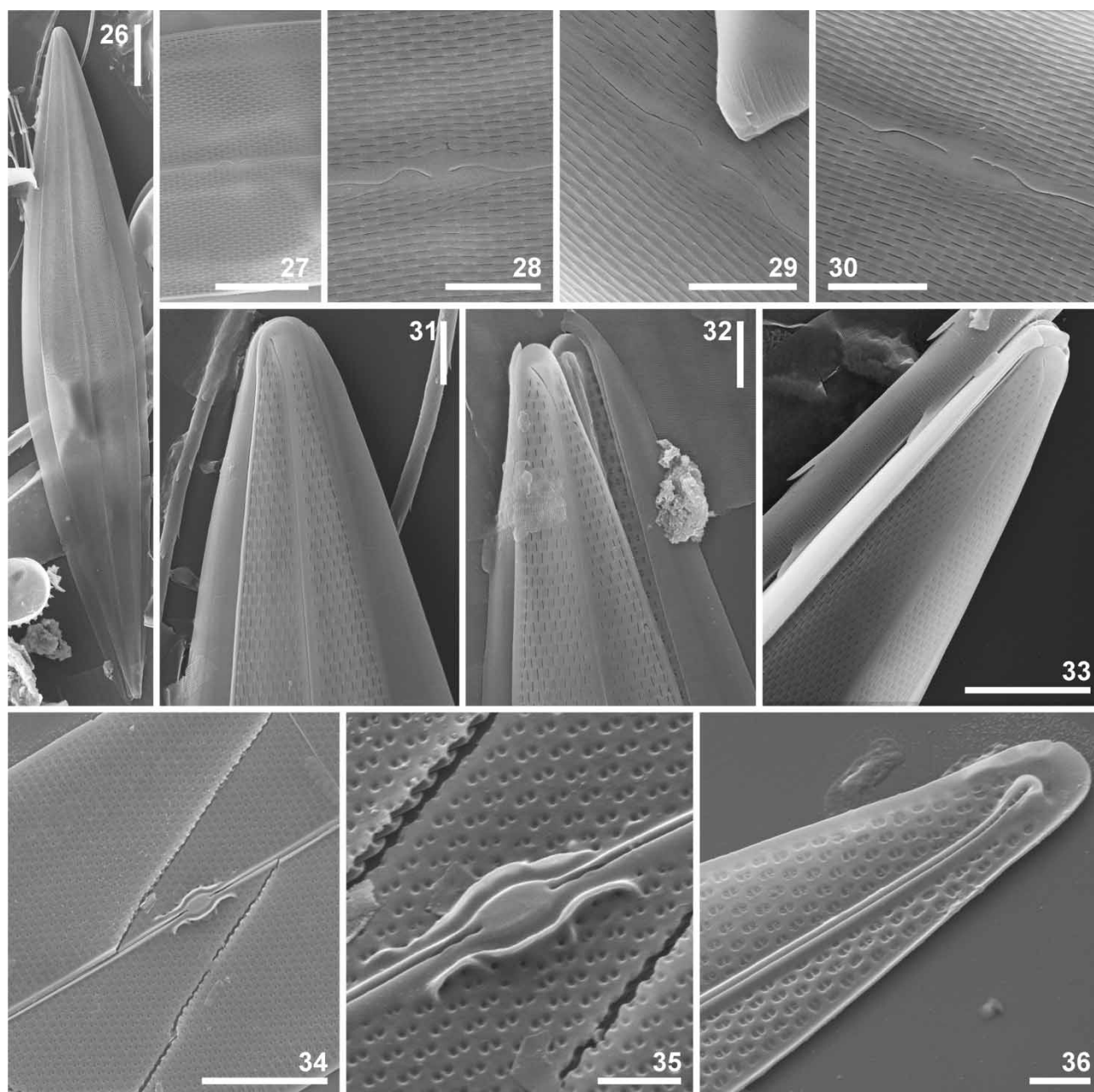


Figs 21–23. *Pleurosigma atlanticum*, LM from lectotype material (Figs 21, 23) and slide 284/48 (Fig. 22). **Figs 24–25.** *Pleurosigma chilense*, LM from lectotype slide (Fig. 24) and isolectotype slide (Fig. 25). **Figs 21–22.** Valve view of two specimens showing striation. **Fig. 23.** Valve apex showing funnel-shaped terminal area in apical position. **Fig. 24.** Valve view of a frustule. **Fig. 25.** Half-frustule showing the stria pattern. Scale bars = 10 μm (Figs 21–22, 24–25); 5 μm (Fig. 23).

valves observed) (Figs 24–26). Raphe–sternum straight, becoming somewhat eccentric at the ends with terminal areas bilaterally dilated, asymmetric, funnel-shaped, in apical position (Fig. 25). Raphe angle 0° . Central area very small, oval, symmetric (Figs 24–25). Central and terminal fissures not visible in LM. Transapical striae parallel 29–33 in 10 μm , oblique striae 27–33 in 10 μm , intersecting at a $51\text{--}59^\circ$ angle.

External and internal details of the raphe only visible in SEM. External central raphe fissures undulated in the same direction (W-shaped), coaxial or slightly displaced

(Figs 27–30). External terminal raphe fissures oppositely bent, delimiting a terminal area with one or two isolated pores (Figs 31–33). Sternum slightly thickened internally, central nodule surrounded by two bars, thick, slightly irregular, with a few siliceous lateral extensions into the interstriae (Figs 34–35). Central raphe endings slightly dilated, coaxial. Helictoglossae turned in opposite directions (Fig. 36). Striae uniseriate, with elliptical areolae, bisected internally by a narrow silica bar (Figs 35–36), and with external apical slit-like foramina (Figs 28–30). At the margin, simple areolae alternate with bisected areolae

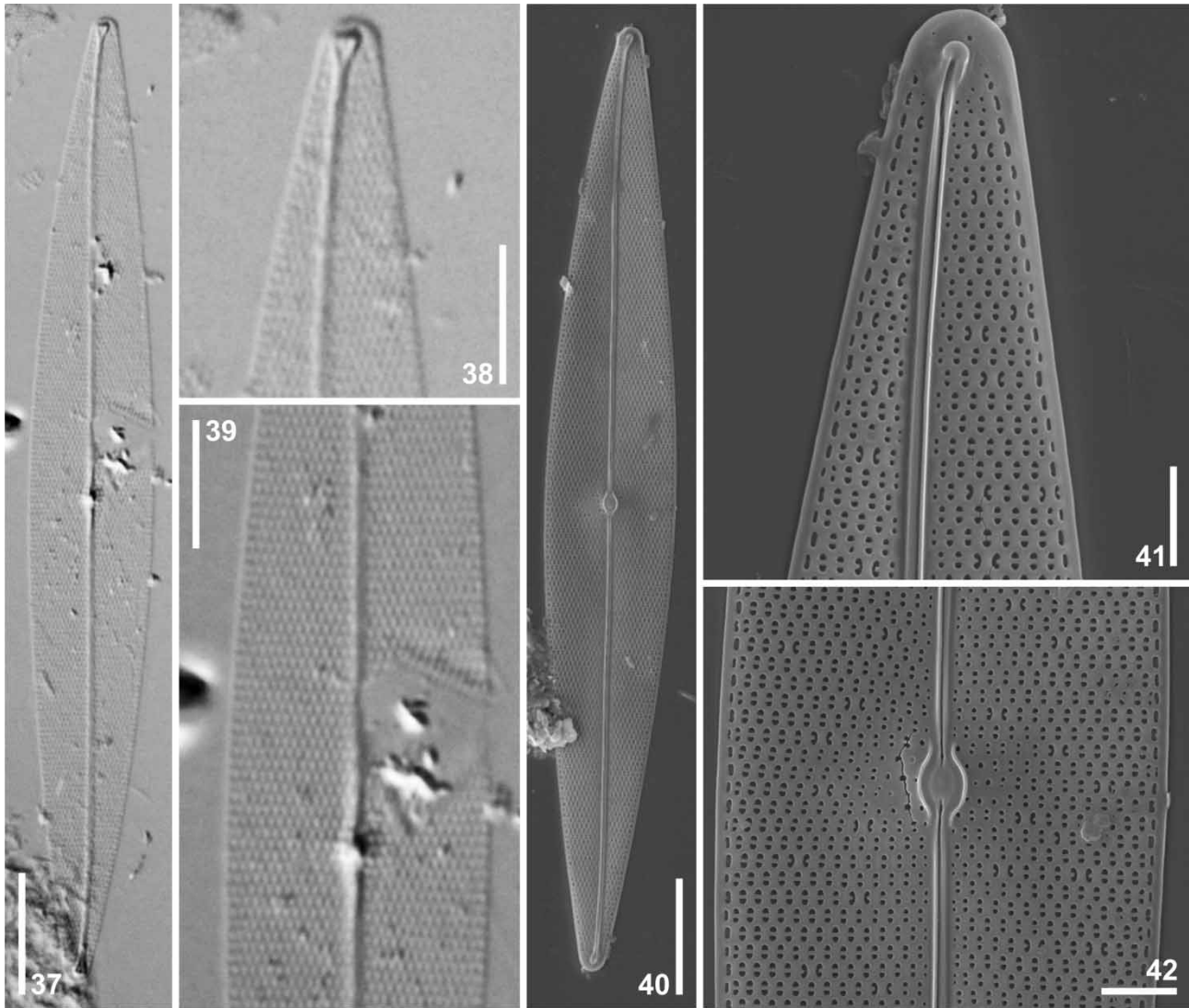


Figs 26–36. *Pleurosigma chilense*, type material, SEM external (Figs 26–33) and internal views (Figs 34–36). **Fig. 26.** Valve view of a frustule. **Fig. 27.** Central part of the valve. **Figs 28–30.** Detail of valve centre showing slit-like foramina and variation in the W-shaped central raphe fissures. **Figs 31–33.** Valve apex showing the terminal raphe fissure. Note the apical funnel-shaped terminal area in Fig. 32. **Fig. 34.** Central region of the valve. **Fig. 35.** Central nodule bordered by two thick bars. Note areolae with velum-type rota. **Fig. 36.** Valve apex showing raphe–sternum and helictoglossa. Scale bars = 10 μm (Fig. 26); 5 μm (Figs 27, 33–34); 2 μm (Figs 28–32); 1 μm (Figs 35–36).

(Fig. 36). Marginal foramina fused or nearly so into a continuous slit (Figs 31–33).

Remarks. This species was described by Hustedt & Krasske (Krasske 1941) as *P. chilensis* and its grammatically incorrect name was corrected to *P. chilense* by Simonsen (1987) in accordance with articles 32.7 and 60.11 of the International Code of Botanical Nomenclature (ICBN) (McNeill

et al. 2006). Simonsen (1987: 265, pl. 395, figs 1–4) selected the slide 297/56, Calbuco, Chile, Plankton, Kr. 4310 in the Hustedt Collection (BRM) as the lectotype of *P. chilense* because other slides labelled Calbuco, Chile Oberflächenplankton 27 November 1937 did not contain the taxon. Subsequently, Lange-Bertalot et al. (1996: 171, pl. 32, figs 2–3) chose another lectotype, D III 326, housed in the Kassel Herbarium, Naturkundemuseum im Ottoneum,



Figs 37–42. *Pleurosigma indicum*, valve from holotype slide in LM (Figs 37–39) and additional type material from sample SM338 in internal SEM view (Figs 40–42). **Fig. 37.** Valve. **Fig. 38.** Valve apex showing the asymmetric funnel-shaped terminal area in apical position. **Fig. 39.** Valve centre. **Fig. 40.** Whole valve. Note raphe–sternum almost straight, slightly curved at the ends and helictoglossae turned in opposite directions. **Fig. 41.** Detail of the valve apex. **Fig. 42.** Valve centre showing proximal raphe ends and nodule bordered by two thin bars. Scale bars = 10 µm (Figs 37, 40); 5 µm (Figs 38–39); 2 µm (Figs 41–42).

Kassel, Germany. Because no holotype was designated (Krasske 1941) and the material selected by Simonsen (1987) is not in conflict with the protologue, his selection must be followed based on article 9.17 of the ICBN.

Pleurosigma indicum Simonsen (Figs 37–42, Table 1)

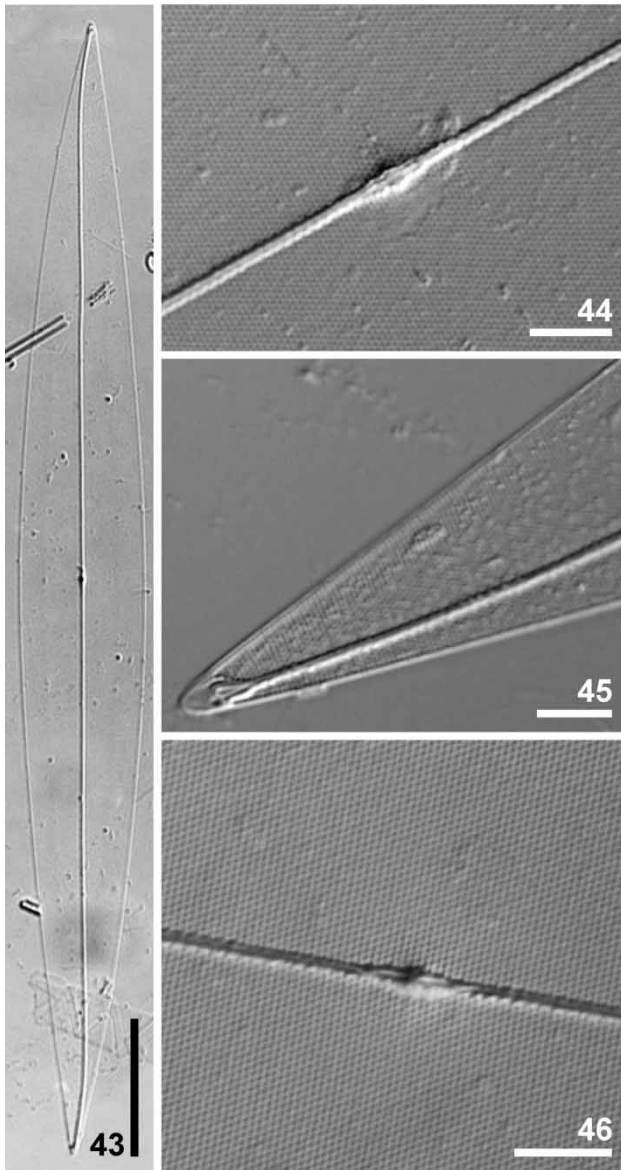
Protologue. Simonsen 1974, p. 46, pl. 29, figs 3a–b.

Description. Valves delicate, lanceolate, slightly sigmoid near the apices, gradually tapering towards the ends, flat, with subacute ends, 79.0–81.5 µm long, 10–11 µm wide (two valves observed) (Figs 37–40). Raphe–sternum almost straight for most part of its length, becoming slightly eccentric towards the ends, with terminal areas asymmetric, funnel-shaped, in apical position (Figs 37–38). Raphe angle +2.5–2.6°. Central area small, oval, symmetric (Figs 37,

39). Central and terminal fissures not visible in LM. Transapical striae parallel 23–24 in 10 µm, oblique striae, 20–24 in 10 µm, intersecting at a 44–48° angle.

Details of the raphe only visible in SEM (one internal valve observed). Sternum thickened internally, central nodule surrounded by two bars, thick and regular (Figs 40, 42). Central raphe endings coaxial (Fig. 42). Helictoglossae turned in opposite directions (Figs 37, 40–41). Internally areolae elliptical, bisected by a siliceous bar over most of the valve and roundish without bars around the central area (Figs 41–42).

Remarks. Simonsen (1974) stated that *P. indicum* was rare to very rare and has probably been overlooked because the valve is very delicate. The material he referred to was carefully examined but only a single additional matching



Figs 43–46. *Pleurosigma simonsenii*, valve from holotype slide (Figs 43–45) and additional material mentioned in the protologue (Fig. 46), LM. **Fig. 43.** Whole valve. **Fig. 44.** Detail of the central area and raphe fissures. **Fig. 45.** Apex showing asymmetric funnel-shaped terminal area in apical position. **Fig. 46.** Central part of a valve showing undulating central raphe fissures. Scale bars = 50 µm (Fig. 43); 5 µm (Figs 44–46).

specimen was found. As far as we can determine this taxon has not been reported since it was first described.

Pleurosigma simonsenii Hasle (Figs 43–46, 54–55, Table 1)

Protologue. Simonsen 1974, p. 46, pl. 30, as *P. planctonicum*. Correct name given by Hasle & Syvertsen 1996, p. 339.

Synonym. *Pleurosigma planctonicum* Simonsen

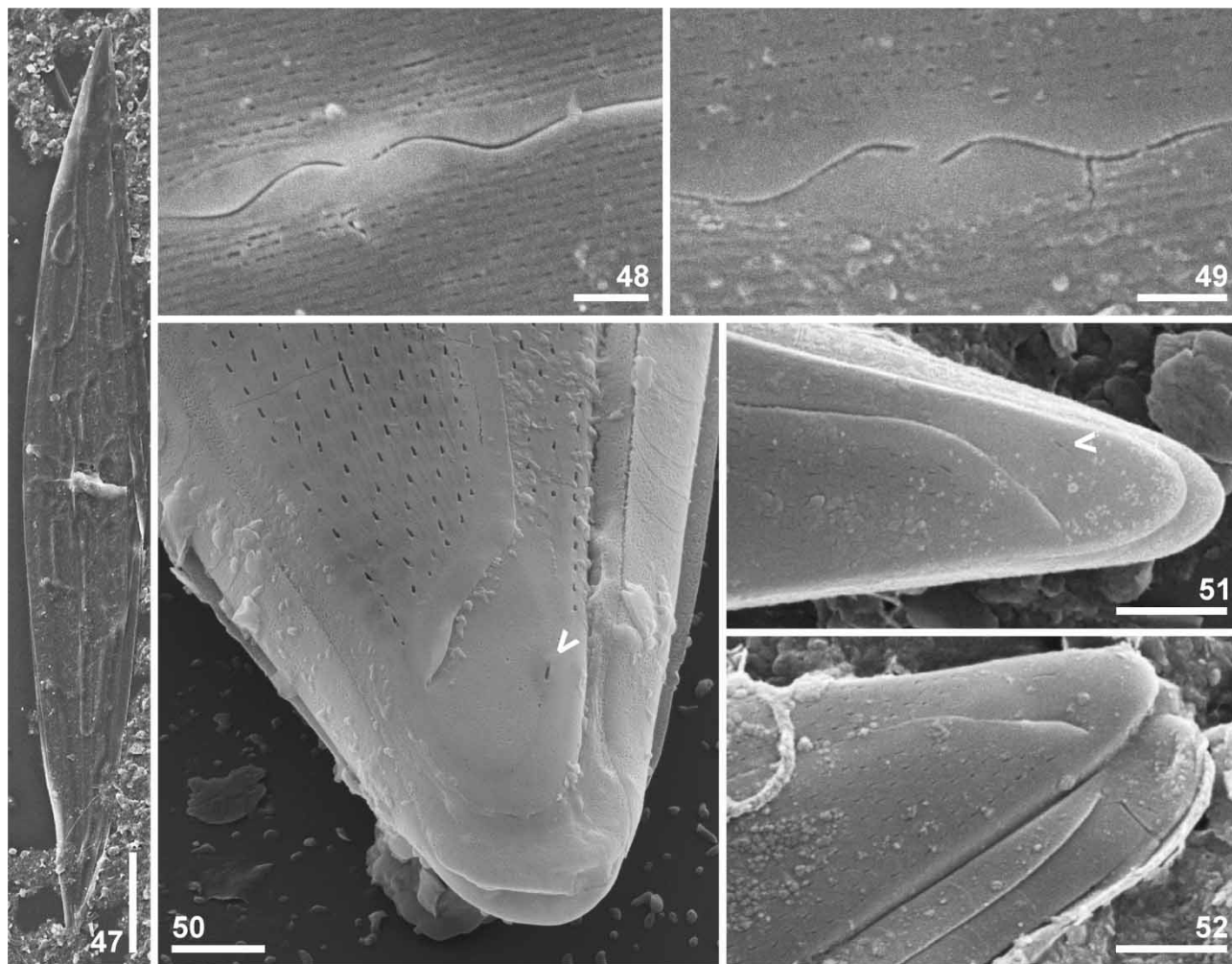
Description. Valves very delicate, lanceolate, only barely sigmoid near the poles, gradually tapering towards the acute ends, only very slightly vaulted, 250–598 µm long, 30–73 µm wide (six valves observed) (Fig. 43). Raphe–sternum straight becoming markedly eccentric at the ends (Fig. 43). Raphe angle +1.6–2.7°. Central area minute (Figs 43–44, 46). External central raphe fissures undulating in the same direction (W-shaped) and hardly visible in LM (Fig. 46). Terminal areas unilaterally dilated, asymmetric funnel-shaped, in apical position, leaving a hyaline apical field (Fig. 45). Transapical striae parallel 30–32 in 10 µm, oblique striae, 26–28 in 10 µm, intersecting at a 56–60° angle.

Sternum slightly thickened internally, central nodule surrounded by two symmetrical bars and central raphe endings coaxial, slightly dilated in SEM (Fig. 54). Helictoglossae turned in opposite direction with no particular additional apical structure (Fig. 55). Striae uniseriate with uniform areolae throughout except for a minute area around the central nodule (Figs 54–55). Internally areolae elliptical, bisected by a siliceous bar over most of the valve and roundish without bars around the nodule (Figs 54–55). A row of areolae with triple siliceous bars alternating with areolae without bars or with one bar around the valve margin (Fig. 55).

Material from Buenos Aires coastal waters (Figs 47–53, 56–58)

Specimens analysed with LM (16 frustules observed) match those of the type material of *P. simonsenii* in size range, valve outline, raphe–sternum curvature, shape of terminal areas, stria density and angle of oblique striae (Table 1). Therefore, we examined some of these in external view (36 valves observed) in SEM for their fine morphology (Figs 47–52) and others in internal view (seven valves observed) for terminal area details (Figs 53, 56–58).

The valves are barely vaulted with the external central raphe fissures undulating in the same direction (W-shaped), coaxial or slightly displaced (Figs 48–49) and the external terminal raphe fissures oppositely bent towards the concave side of the raphe–sternum (Figs 50–52), delimiting a smooth terminal area interrupted by a small fissure situated at the convex side of the raphe–sternum (Figs 50–51, arrowheads). This small fissure corresponds internally to a small group of areolae (Figs 55, 57–58, arrowheads). The Buenos Aires specimens matched those from the Simonsen's sample SM603, except for one feature. In Simonsen material, there is a row of areolae with triple siliceous bars alternating with areolae without bars or with only a single bar at the valve margin (Fig. 55). In the specimens from the Argentinian material, simple areolae and areolae with a bar alternate irregularly (Figs 56–58). Since only one internal view of a single specimen was found in the type material, we cannot assess the variability of this feature in that population, nor has such variability been observed in the many *Pleurosigma* species examined in SEM. Otherwise, the Argentinian specimens fully match



Figs 47–52. *Pleurosigma simonsenii*, material from Mar Azul, Province of Buenos Aires, Argentina, SEM, external views. **Fig. 47.** Collapsed cell showing the ribbon-shaped chloroplast. **Figs 48–49.** Valve centre showing raphe fissures. **Figs 50–52.** Apical region of frustule showing terminal raphe fissures. Note the small slit on the convex side of the raphe–sternum (arrowheads). Scale bars = 50 µm (Fig. 47); 2 µm (Figs 51–52); 1 µm (Figs 48–50).

the type specimen, including such fine details as the small group of areolae seen in the internal apical aspect; therefore the Argentinian specimens are here assigned to the same species.

Remarks. *Pleurosigma planctonicum* Simonsen (1974) is a later homonym of *P. planctonicum* Cleve-Euler (1917). Thus, in order to resolve the homonymy Hasle (Hasle & Syvertsen 1996) proposed a new name for the later homonym: *Pleurosigma simonsenii* Hasle.

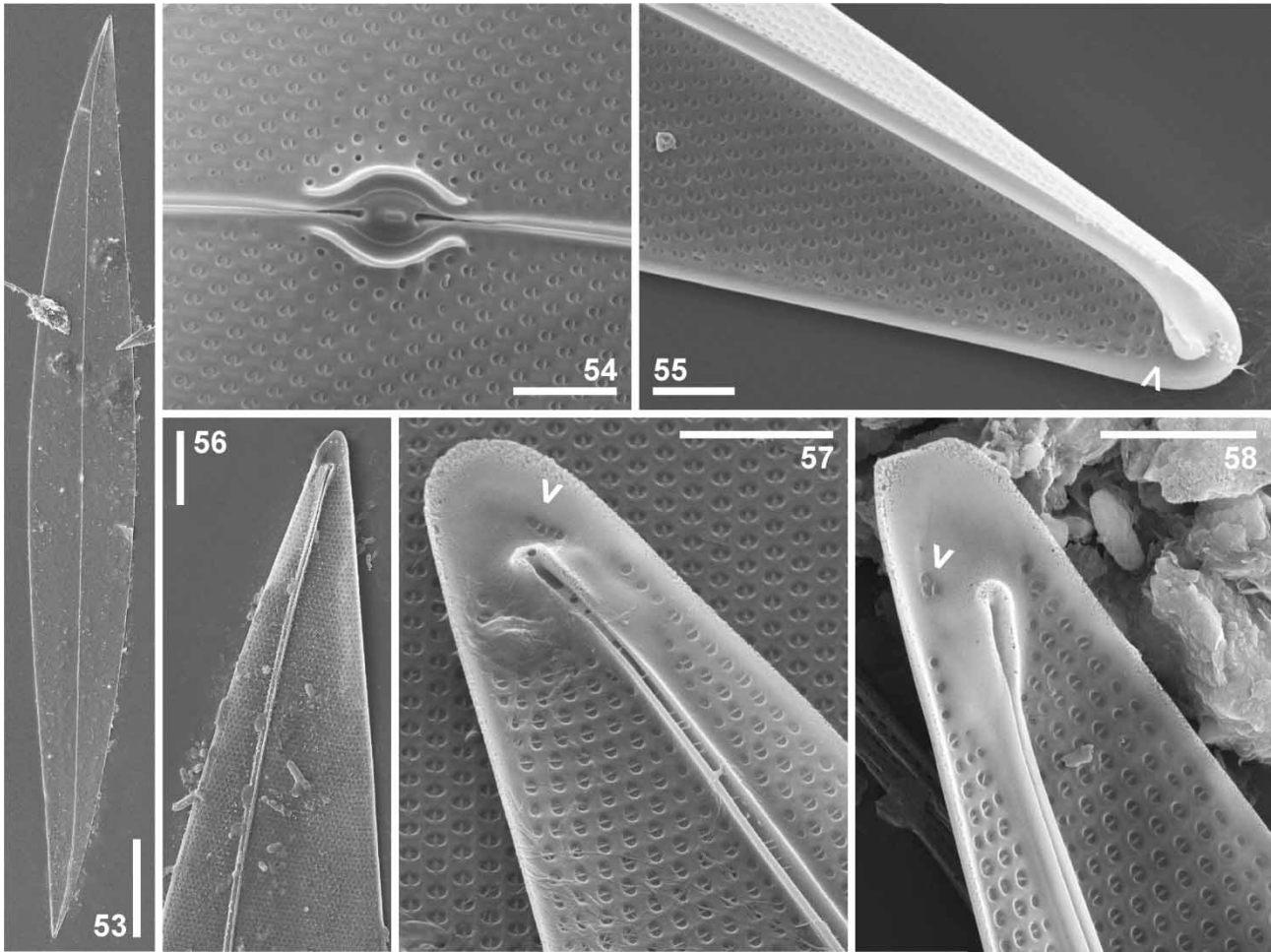
Simonsen (1974) pointed out in the protologue that the species was very rare to rare in the material from stations 209 to 218 and only a single additional matching specimen was found in SM603 from station 217, here illustrated in Figs 54–55. Because of the small number of specimens available, the ultrastructural features of the external valve surface and complementary details of the internal view were obtained from the additional material collected in Mar Azul (37°21'25"S by 57°01'49"W), Province of Buenos

Aires, Argentina. The species was also found in the Western English Channel by Boalch & Harbour (1977) and its identity was confirmed by the examination of slide PA2/93 in the Hustedt collection (BRM). The species has also been observed from Port Hacking, New South Wales, Australia, in a sample from the Stidolph collection deposited in the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand.

Pleurosigma patagonicum (Ferrario & Sar) Sterrenburg & Sar stat. nov. (Figs 59–76, Table 1)

Synonym. *Pleurosigma chilensis* var. *patagonica* Ferrario & Sar 1990, p. 201, figs 1–6.

Description. Valves narrowly lanceolate to sub-rhomboidal, straight, tapering gradually towards the acute apices, slightly vaulted near the ends (Figs 59, 63–64), 189–229 µm long, 17–20.6 µm wide (36 valves found). Raphe–sternum straight (Figs 59, 63–64). Terminal areas bilaterally dilated,



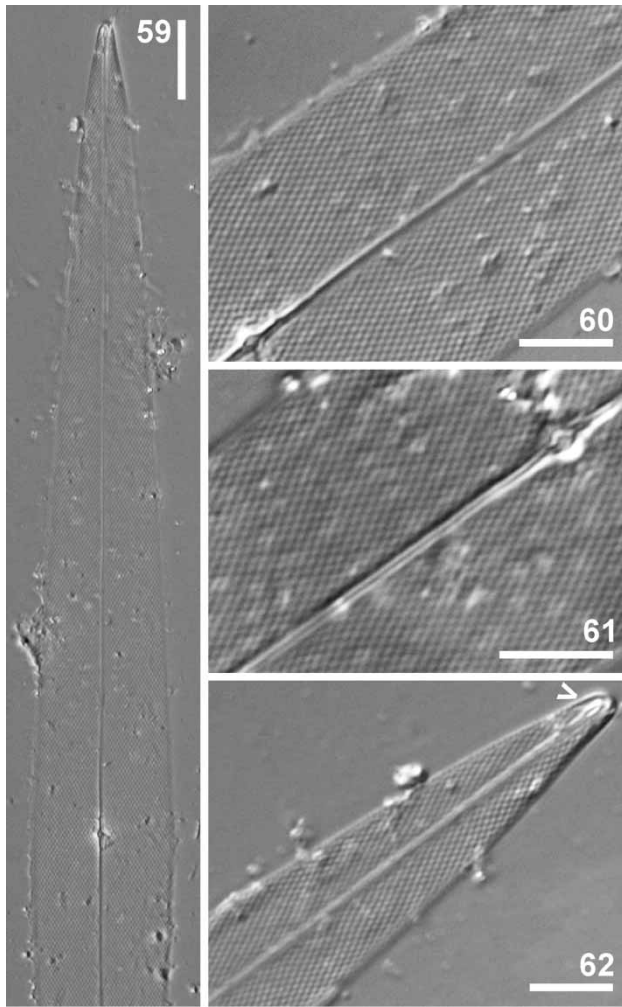
Figs 53–58. *Pleurosigma simonsenii*, material from Mar Azul, Province of Buenos Aires, Argentina (Figs 53, 56–58) and additional material listed in the protologue (Figs 54–55), SEM internal views. **Fig. 53.** Whole valve. **Fig. 54.** Valve centre showing proximal raphe ends and nodule bordered by two thin bars. **Fig. 55.** Apex with terminal area and helictoglossa. Note valve surface vaulted near the apex and small areolae corresponding to a short external apical slit. **Fig. 56.** Part of the valve where the raphe–sternum becomes eccentric. **Figs 57–58.** Valve apex showing unilaterally dilated terminal area. Note the small group of areolae (arrowheads) on the convex side of the raphe–sternum. Scale bars = 50 μm (Fig. 53); 5 μm (Fig. 56); 2 μm (Figs 54–55, 57–58).

symmetric, funnel-shaped, in apical position visible in LM (Figs 59, 62), with a calcar on one side (Fig. 62, arrowhead). Raphe angle 0° . Central area very small, orbicular, symmetric (Figs 59–61). Central and terminal raphe fissures not visible in LM. Transapical striae parallel 26–30 in $10\mu\text{m}$, oblique striae 23–26 in $10\mu\text{m}$ at the centre and 23–29 in $10\mu\text{m}$ at the poles. Oblique striae intersecting at $57\text{--}66^\circ$ and $56\text{--}62^\circ$ angles at the valve centre and poles, respectively.

External and internal details of the raphe only visible in SEM (34 valves observed). External central raphe fissures projected for a long distance into the central area, undulated, overlapped (Figs 65–68). External terminal raphe fissures long, hook-shaped, slightly eccentric, curved around the apices both in the same direction (Figs 69–70, 75–76, arrowheads). Sternum slightly thickened internally, central nodule surrounded by two symmetrical bars, central raphe endings coaxial and slightly dilated in pore-like

expansions (Figs 72–74). Internally, apices with one or two isolated pores in apical position and two rows of slits, placed laterally at the last section of raphe–sternum towards the helictoglossae (Figs 71, 74–76) and externally visible as two subtle fissures, calcars (Figs 69–71). Internally areolae elliptical, bisected by a siliceous bar over most of the valve (Figs 72–74), roundish without bars in a rectangular area around the central nodule (Figs 72–73). Areolae opening externally as apically oriented slit-like foramina (Figs 65–70).

Remarks. This taxon was first described as *P. chilensis* var. *patagonica*, but must be raised to species rank. *Pleurosigma patagonicum* and *P. chilense* cannot be easily separated in LM, but the differences in SEM warrant separate taxonomic status. The external central raphe endings are only slightly curved and almost touching in *P. patagonicum* but markedly curved, W-shaped and clearly separated in



Figs 59–62. *Pleurosigma patagonicum*, valve from holotype slide (Figs 59, 60, 62) and additional material listed in the protologue (Fig. 61), LM. **Fig. 59.** Whole valve. **Fig. 60.** Part of the valve showing striation. **Fig. 61.** Valve centre showing small, orbicular and symmetric central area. **Fig. 62.** Apex showing symmetric, funnel-shaped terminal area in apical position and calcar (arrowhead). Scale bars = 10 µm (Fig. 59); 5 µm (Figs 60–62).

P. chilense. Two rows of slits running to the apex on both sides of the valve are present in *P. patagonicum* but there is none in *P. chilense*. In *P. patagonicum*, a rather large field is present near the centre where the areolae are simple and round, while this area is not present in *P. chilense* and the areolae are crossed by a bar. Finally, *P. patagonicum* is much narrower than *P. chilense*. As far as we can determine *P. patagonicum* has not been reported since it was described.

Discussion

Hendey (1964) designated the slide BM 23654 as the type material of *P. intermedium* and, since no holotype was explicitly designated by Smith (1853), this slide is the lectotype. Similarly, Hendey (1964) examined *P. nubecula* on

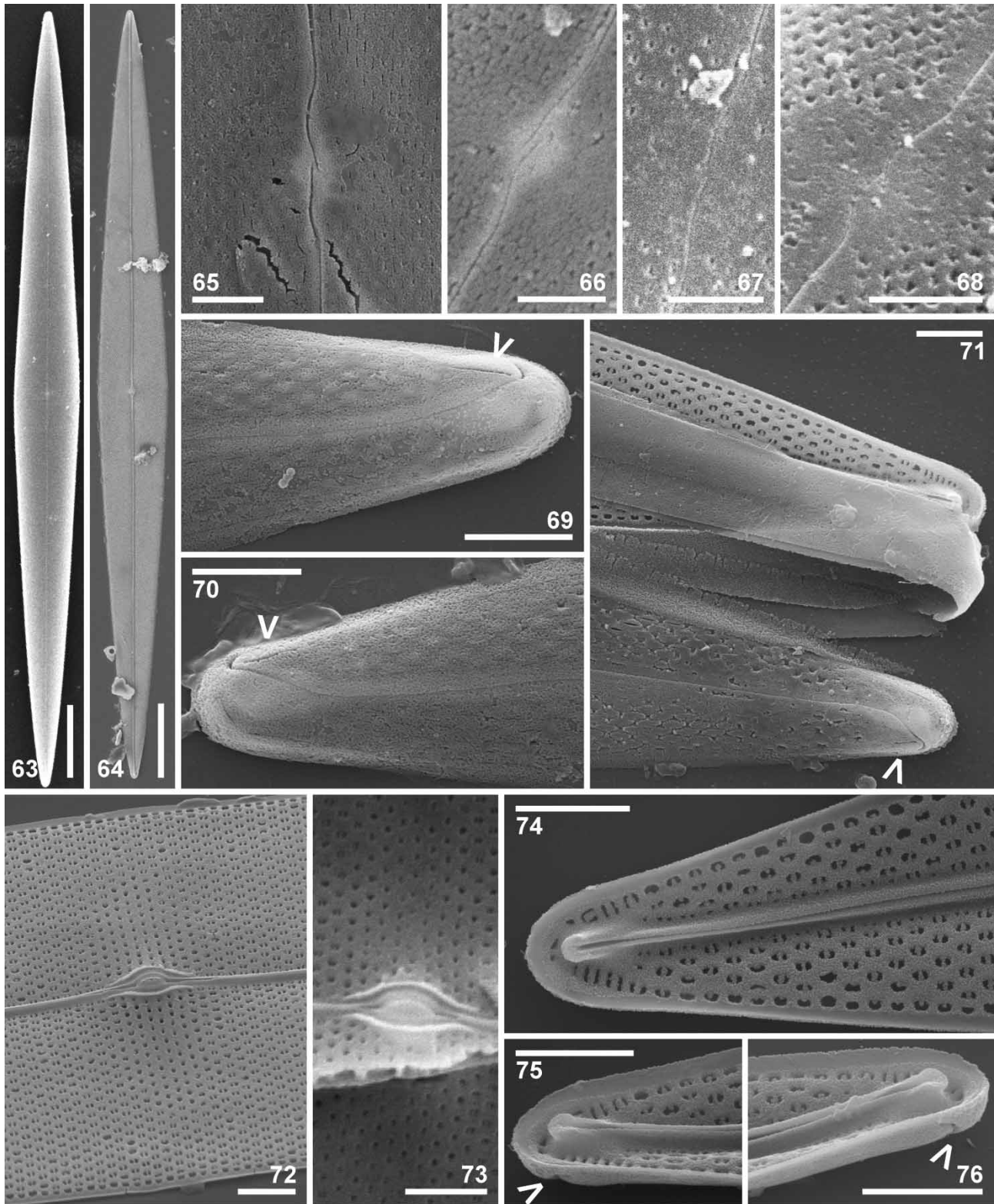
BM 23656 slide and stated that ‘material ...marked Sussex, March, 1852, is presumed to be of the type material mentioned by W. Smith *loc. cit.* as Seaford, Sussex, Mar. 1852’, and thus should also be considered a lectotype. However, when comparing *P. intermedium* and *P. nubecula* in LM, Hendey (1964) concluded that they should be regarded as conspecific ‘until it is possible to show that there exists some structural character that would separate them’. The correct name is *P. intermedium* which ‘is the earlier by virtue of pride of place’ (Hendey 1964). Our comparative LM analysis of the isolectotypes of these taxa revealed some differences in morphometric data, but more importantly, SEM analysis of unmounted material did not reveal any relevant morphological differences between the taxa. The SEM findings thus support Hendey’s (1964) decision to include *P. nubecula* as a heterotypic synonym of *P. intermedium*.

The protologue of *P. atlanticum* Heiden & Kolbe (1928) was published in June and that of *P. atlanticum* Frenguelli (1928) published in December, given its publication priority, the epithet *atlanticum* must apply to the species described by Heiden & Kolbe, and the later homonym requires a new name. We have not yet found specimens that correspond to the Frenguelli’s (1928) description on slides of the series 167 (Frenguelli Collection, LPC). Further investigation is being undertaken in the area mentioned by Frenguelli to obtain material containing specimens matching the description of this taxon.

The comparison between the type material of *P. chilense* and that of the taxon described by Ferrario & Sar (1990), revealed several major differences in the morphological characters. In LM, the taxa only differ in the valve outline and curvature of the raphe–sternum towards the ends, but they are clearly separated by the fine morphology of the apical area, the central and terminal raphe fissures and the velum of the areolae around the central area and on the marginal row. Therefore, Ferrario & Sar’s (1990) taxon cannot be considered a variety of *P. chilense* and is raised to species rank as *P. patagonicum*.

Pleurosigma patagonicum resembles *P. acus* Mann in having a narrowly lanceolate to sub-rhombic valve outline with acute apices, a straight raphe–sternum and being of the same size. Nevertheless, based on a comparison of the type material of *P. patagonicum* and the syntype and holotype of *P. acus* (Stidolph 2002: 273, figs 1–4), there are several major differences. The transapical and oblique stria density is higher in *P. patagonicum* (transapical 24–30, oblique 24–29 in 10 µm) than in *P. acus* (transapical 20, oblique 17 in 10 µm), the stria angle is considerably smaller in *P. patagonicum* (57–64°) than in *P. acus* (80–90°), and whilst *P. patagonicum* has calcars, *P. acus* does not.

Pleurosigma simonsenii from Port Hacking, New South Wales, Australia, was provisionally identified as *P. chilense* in material from the Stidolph collection. Based on more information, these species are easily separated by a large discontinuity in size range (300–600 µm in length and



Figs 63–76. *Pleurosigma patagonicum*, holotype material, SEM external (Figs 63, 65–71) and internal views (Figs 64, 72–76). **Figs 63–64.** Whole valve. **Figs 65–68.** Variability in the central raphe fissures. **Figs 69–70.** Valve apices of the same specimen showing raphe fissures curved in the same direction. Note calcars (arrowheads). **Fig. 71.** Broken frustule at apex showing calcar (arrowhead) and helictoglossa. **Fig. 72.** Valve centre showing nodule and transapical striae consisting of roundish areolae with velum. **Fig. 73.** Fractured valve at centre showing coaxial raphe endings and nodule bordered by two thin siliceous bars. **Fig. 74.** Valve apex showing apical structure and helictoglossa. **Figs 75–76.** Tilted valve at apex showing external terminal raphe fissures bent in the same direction (arrowheads). Scale bars = 20 μm (Figs 63–64); 2 μm (Figs 65–76).

40–73 µm in width in *P. simonsenii* and 103–140 µm in length and 15–20 µm in width in *P. chilense*) and differences in the raphe angle, with +1.3 to 3.1° in *P. simonsenii* and 0° in *P. chilense*. Additionally, the valve outline is somewhat sigmoid in *P. simonsenii* but almost straight in *P. chilense*, with more acute apices in the former.

Pleurosigma indicum cannot be confused with the other species treated here because of major differences in many characters, apart from a straight aspect.

Summarizing these findings, *P. atlanticum*, *P. chilense*, *P. indicum*, *P. intermedium* and *P. simonsenii* are valid species, whereas *P. nubecula* is a heterotypic synonym of *P. intermedium* while *P. chilensis* var. *patagonica* is raised to species rank as *P. patagonicum*, differentiating in several major features from *P. chilense*.

Despite the usual description of *Pleurosigma* species as being sigmoid in shape, the straight species described here show the essential characters of the genus: valve with slit-like external foramina, round to oval internal areolae with transverse bars and a distinctive oblique striation crossed by transapical striae. There is a strong variation in the valve sigmoidicity between the different *Pleurosigma* species as opposed to a very small variability within species.

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References

- BOALCH G.T. & HARBOUR D.S. 1977. Observations on the structure of a planktonic *Pleurosigma*. *Nova Hedwigia* 54: 275–280.
- BOYER C.S. 1927. Synopsis of North American Diatomaceae, Part II. Naviculatae, Surirellatae. *Proceedings of the Academy of Natural Sciences of Philadelphia, Supplement* 79: 229–583.
- CARDINAL A., POULIN M. & BÉRARD-TERRIAULT L. 1986. Les diatomées benthiques de substrats durs des eaux marines et saumâtres du Québec 5. Naviculales, Naviculaceae; les genres *Donkinia*, *Gyrosigma* et *Pleurosigma*. *Naturaliste canadien* 113: 167–190.
- CARDINAL A., POULIN M. & BÉRARD-TERRIAULT L. 1989. New criteria for species characterization in the genera *Donkinia*, *Gyrosima* and *Pleurosigma* (Naviculaceae, Bacillariophyceae). *Phycologia* 28: 15–27.
- CLEVE P.T. 1894. Synopsis of the naviculoid diatoms. Part I. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 26: 1–194.
- CLEVE P.T. & GRUNOW A. 1880. Beiträge zur Kenntniss der arctischen Diatomeen. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 17: 1–121.
- CLEVE-EULER A. 1917. Quantitative plankton researches in the Skagerrak. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 57: 1–130.
- COMPÈRE P. 1999. Report of the committee for algae: 5. *Taxon* 48: 129–132.
- FERRARIO M.E. & SAR E.A. 1990. Ultraestructura de *Pleurosigma chilensis* var. *patagonica* nov. var. (Bacillariophyceae). *Darwiniana* 30: 201–204.
- FERRARIO M.E., SAR E.A. & SALA S.E. 1995. Metodología básica para el estudio del fitoplancton con especial referencia a las diatomeas. In: *Manual de métodos ficológicos* (Ed. by K. Alveal, M.E. Ferrario, E.C. Oliveira & E. Sar), pp. 1–23. Universidad de Concepción, Concepción.
- FRENGUELLI J. 1928. Diatomeas del Océano Atlántico frente a Mar del Plata (República Argentina). *Anales Museo Nacional de Historia Natural 'Bernardino Rivadavia'* 34: 497–572.
- GREUTER W., MCNEILL J., BARRIE F.R., BURDET H.M., DEMOULIN V., FILGEIRAS T.S., NICOLSON D.H., SILVA P.C., SKOG J.E., TREHANE P., TURLAND N.J. & HAWKSWORTH D.L. 2000. International Code of Botanical Nomenclature (St. Louis Code) adopted by the Sixteenth International Botanical Congress St Louis, Missouri, July–August 1999. *Regnum Vegetabile* 138: 1–474.
- HASLE G.R. & SYVERTSEN E.E. 1996. Marine diatoms. In: *Identifying marine phytoplankton* (Ed. by C.R. Tomas), pp. 5–385. Academic Press, San Diego.
- HEIDEN H. & KOLBE R.W. 1928. Die marinen Diatomeen der Deutschen Südpolar-Expedition 1901–3. *Deutsche Südpolar-Expedition* 8: 447–715.
- HENDEY N.I. 1964. *An introductory account of the smaller algae of British coastal waters. Part V. Bacillariophyceae (diatoms)*. Her Majesty Stationery Office, London. 317 pp.
- KRASSKE G. 1941. Die Kieselalgen des chilenischen Küstenplanktons. *Archiv für Hydrobiologie* 38: 268–287.
- LANGE-BERTALOT H., KÜLS K., LAUSER T., NÖRPEL-SCHEMP M. & WILLMANN M. 1996. Diatom taxa introduced by Georg Krasske. Documentation and revision. *Iconographia Diatomologica* 3: 1–358.
- LANJOUW J., BAEHNI CH., ROBYNS W., ROLLINS R.C., ROSS R., ROUSSEAU J., SCHULZE G.M., SMITH A.C., DE VILMORIN R. & STAFLEU F.A. 1956. International Code of Botanical Nomenclature (Paris code) adopted by the Eighth International Botanical Congress, Paris, July 1954. *Regnum Vegetabile* 8: 1–338.
- MCNEILL J., BARRIE F.R., BURDET H.M., DEMOULIN V., HAWKSWORTH D.L., MARHOLD K., NICOLSON D.H., PRADO J., SILVA P.C., SKOG J.E., WIERSEMA J.H. & TURLAND N.J. 2006. International Code of Botanical Nomenclature (Vienna Code). Adopted by the Seventeenth International Botanical Congress Vienna, Austria, July 2005. *Regnum Vegetabile* 146: 1–568.
- PERAGALLO H. 1891. Monographie du genre *Pleurosigma* et des genres alliés. *Le Diatomiste* 1: 1–35.
- PERAGALLO H. & PERAGALLO M. 1897–1908. *Diatomées marines de France et des districts maritimes voisins*. M.J. Tempère Micrographe-Éditeur, Grez-sur-Loing. 492 pp., 137 pls.

- PRITCHARD A. 1861. *History of Infusoria, including the Desmidiaceae and Diatomaceae British and foreign*. Edition four, enlarged and revised by J.T. Arlidge, W. Archer, J. Ralfs, W.C. Williamson and the author. Whittaker & Co, London. 368 pp., 40 pls.
- PRYGIEL J. & COSTE M. 2000. *Guide méthodologique pour la mise en oeuvre de l'indice biologique diatomées*. Agences de l'Eau, Ministère de l'Aménagement du Territoire et de l'Environnement, Direction de l'Eau & CEMAGREF, Paris. 134 pp.
- REID G. 2001. On the identity of *Pleurosigma angulatum* (Bacillariophyta) and related species. *Bulletin of the Natural History Museum, Botany Series* 31: 107–117.
- REID G. 2002. Four new species of *Pleurosigma* (Bacillariophyta) from Alexandria, Egypt. *Botanical Journal of the Linnean Society* 140: 77–92.
- ROSS R. & STERRENBURG F.A.S. 1996. Proposal to conserve the name *Navicula angulata* E. J. Quekett (*Pleurosigma angulatum* (E. J. Quekett) W. Sm.) (Bacillariophyta) with a conserved type. *Taxon* 45: 121–122.
- ROSS R., COX E.J., KARAYEVA N.I., MANN D.G., PADDOCK T.B.B., SIMONSEN R. & SIMS P.A. 1979. An amended terminology for the siliceous components of the diatom cell. *Beihefte zur Nova Hedwigia* 64: 513–533.
- ROUND F.E., CRAWFORD R.M. & MANN D.G. 1990. *The diatoms. Morphology and biology of the genera*. Cambridge University Press, Cambridge. 747 pp.
- SAR E.A., SALA S.E., SUNESEN I., HENNINGER M.S. & MONTASTRUC M. 2009. Catálogo de los géneros, especies y taxa infraespecíficos erigidos por J. Frenguelli/Catalogue of the genera, species, and infraspecific taxa erected by J. Frenguelli. *Diatom Monographs* 10: 1–419.
- SIMONSEN R. 1974. The diatom plankton of the Indian Ocean Expedition of R/V 'Meteor' 1964–1965. 'Meteor' *Forschungsergebnisse, Reihe D* 19: 1–107.
- SIMONSEN R. 1987. *Atlas and catalogue of the diatom types of Friedrich Hustedt*. J. Cramer, Berlin. 525 pp., 772 pls.
- SIMONSEN R. 1992. The diatom types of Heinrich Heiden in Heiden & Kolbe 1928. *Bibliotheca Diatomologica* 24: 1–86.
- SMITH W. 1852. Notes on the Diatomaceae; with description of British species included in the genus *Pleurosigma*. *Annals and Magazine of Natural History* 2: 1–12.
- SMITH W. 1853. *A synopsis of the British Diatomaceae; with remarks on their structure, functions and distribution; and instructions for collecting and preserving specimens*. 1. John Van Voorst, London. 89 pp., 32 pls.
- SMITH W. 1856. *Synopsis of the British Diatomaceae; with remarks on their structure, functions and distribution; and instructions for collecting and preserving specimens*. 2. John Van Voorst, London. 107 pp., 32 pls.
- STERRENBURG F.A.S. 1991a. Studies on the genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae). Light microscopical criteria for taxonomy. *Diatom Research* 6: 367–389.
- STERRENBURG F.A.S. 1991b. Studies on the genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae). The *typus generis* of *Pleurosigma*, some presumed varieties and imitative species. *Botanica Marina* 34: 561–573.
- STERRENBURG F.A.S. 2001. Studies on the genera *Gyrosigma* and *Pleurosigma*. The types of Shadbolt and related taxa. *Proceedings of the Academy of Natural Sciences of Philadelphia* 151: 121–127.
- STERRENBURG F.A.S., TIFFANY M.A. & LANGE C.B. 2000. Studies on the genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae). Species from the Salton Sea, California, U.S.A., including *Pleurosigma ambrosianum*, nov. sp. *Proceedings of the Academy of Natural Sciences of Philadelphia* 150: 305–313.
- STERRENBURG F.A.S., MEAVE DEL CASTILLO M.E. & TIFFANY M.A. 2003. Studies on the genera *Gyrosigma* and *Pleurosigma* (Bacillariophyceae): *Pleurosigma* species in the plankton from the Pacific coast of Mexico, with the description of *P. gracilitatis* sp. nov. *Cryptogamie, Algologie* 24: 291–306.
- STIDOLPH S.R. 1992. Observations and remarks on the morphology and taxonomy of the diatom genera *Gyrosigma* Hassall and *Pleurosigma* W. Smith III. *Gyrosigma sterrenburgii* sp. nov., and *Pleurosigma amara* sp. nov. *Diatom Research* 7: 345–366.
- STIDOLPH S.R. 2002. Observations and remarks on the morphology and taxonomy of the diatom genera *Gyrosigma* Hassall and *Pleurosigma* W. Smith. V. *Pleurosigma* types of A. Mann (1925): a critical re-investigation. *Micropaleontology* 48: 273–284.
- VAN HEURCK H. 1880–1885. *Synopsis des diatomées de Belgique*. H. Van Heurck, Anvers. 235 pp., 135 pls.
- VANLANDINGHAM S.M. 1978. *Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Part VI: Neidium through Rhoicosigma*. J. Cramer, Vaduz. pp. 2964–3605.
- VON QUILLFELDT C.H. 2000. *Pleurosigma tenuiforme* spec. nov.; a marine *Pleurosigma* species with long, slender apices, occurring in Arctic regions. *Diatom Research* 15: 221–236.